Journal of Field Ornithology

J. Field Ornithol. 83(4):381–390, 2012 DOI: 10.1111/j.1557-9263.2012.00388.x

Comparing the precision, accuracy, and efficiency of branch clipping and sweep netting for sampling arthropods in two Jamaican forest types

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Received 22 January 2012; accepted 23 July 2012

ABSTRACT. Devising methods for sampling arthropods presents many challenges, including understanding possible differences in results obtained by different individuals (precision), investigating differences between estimates and the actual variable of interest (accuracy), and assessing the effort and cost of a given method (efficiency). We assessed the precision, accuracy, and efficiency of sweep netting and branch clipping, two common methods of sampling arthropods, in mangrove and second-growth scrub forests in Jamaica, West Indies, in 2009. Three individuals used both methods sequentially to sample arthropods in the territories of American Redstarts (*Setophaga ruticilla*). We found that both branch clipping and sweep netting lacked precision because different individuals produced different estimates of either arthropod abundance (number of individuals per sample) or biomass. In both forests, more arthropods were sampled with sweep netting, in terms of biomass and abundance, and several orders of arthropods were collected that were missed by branch clipping. We also detected the absence of a predictable habitat-based difference in arthropod biomass with sweep netting, but not with branch clipping. Sweep netting took longer overall (field and processing time combined) and was therefore less efficient. Despite problems with precision and efficiency, our results suggest that sweep netting may be a more accurate method than branch clipping for sampling foliage arthropods in some forest habitats. Our study also reveals the importance of recognizing and controlling for individual bias and of choosing arthropod sampling methods most appropriate to each study species and habitat type.

RESUMEN. **Comparando la precisión, exactitud y eficiencia de corte de ramas y redes de barrido para muestrear artrópodos en dos tipos de bosques de Jamaica**

El desarrollar métodos para muestrear artrópodos presenta muchos retos, incluyendo el comprender posibles diferencias en los resultados obtenidos por diferentes individuos (precisión), el investigar las diferencias entre estimados y las variables de interés (exactitud) y determinado esfuerzo y costo de un método particular (eficiencia). Pusimos a prueba la precisión, exactitud y eficiencia del corte de ramas y el uso de redes de barrido, que son dos métodos comunes para muestrear artrópodos. El trabajo se llevó a cabo en mangles y matorrales secundarios en Jamaica, Indias Occidentales, en el 2009. Tres personas utilizaron ambos métodos de forma secuencial, para muestrear artrópodos en los territorios de individuos de *Setophaga ruticilla*. Se encontró que ambos métodos carecían de precisión, debido a que distintas personas produjeron diferentes estimados en la abundancia de artrópodos (número de individuos/muestra) y en su biomasa. En ambos tipos de bosques, se muestrearon mayor cantidad de artrópodos con las redes de barrido, en términos de biomasa y abundancia, mientras que fueron dejados fuera varios órdenes al utilizarse el método de corte de ramas. También detectamos la ausencia de una diferencia predecible de hábitat en la biomasa de artrópodos con las redes de barrido, pero no así con el corte de ramas. Las redes de barrido tomaron más tiempo (trabajo de campo y el periodo para procesar los datos) y por lo tanto resultaron menos eficientes. Pese a los problemas de precisión y eficiencia, nuestros resultados sugieren que el método de barrido es más exacto que el corte de ramas para muestrear los artrópodos en el follaje en algunos hábitats de bosque. Nuestro estudio también revela la importancia de reconocer y controlar el sesgo individual y el seleccionar el método de muestreo mas apropiado para un hábitat y el estudio de especies en particular.

Key words: American Redstart, food availability, insect sampling, sampler bias, *Setophaga ruticilla*

To understand how animals interact with their environment and with con- and heterospecifics, determining the availability of their food resources is often necessary. Because many birds feed almost exclusively on arthropods (Gill 2006), ornithologists have studied how arthropod availability relates to such diverse

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topics as bird distributions (Karr 1976, Johnson and Sherry 2001), changes in forest succession (Smith and Robertson 2008), forest fragmentation (Burke and Nol 1998), avian reproduction (Murphy 1986, Rodenhouse and Holmes 1992), overwinter condition (Brown and Sherry 2006a, b, Studds and Marra 2005, 2007), and the timing of migration (Studds and Marra 2007). Despite such studies, sampling arthropods accurately remains challenging due to both the diversity of arthropod life histories (e.g., flying vs. sessile forms) and the substrates on which they are found.

Different methods may be better for sampling different taxa. For example, pitfall traps work well for ground-dwelling arthropods, whereas malaise and sticky traps are efficient at capturing flying arthropods (Morris 1960, Southwood 1978, Cooper and Whitmore 1990). Sampling arthropods in forest habitats is particularly challenging because of the diversity of plant species and complexity of the vegetative structure. Vacuums and other suction devices, branch clipping, and sweep netting have traditionally been used to sample foliage-dwelling arthropods in forest habitats (Cooper and Whitmore 1990, Buffington and Redak 1998). Although each arthropod sampling method has advantages and disadvantages, all methods potentially suffer from difficulties associated with matching sampling with perceptions of availability of birds (Hutto 1990, Sherry et al. 2005), measurement of just standing crop versus productivity (Hutto 1990), an overly taxon-specific focus (Cooper and Whitmore 1990), and a patchy distribution of arthropods (Majer et al. 1990).

The precision, accuracy, and efficiency of arthropod sampling methods have rarely been assessed. For example, sweep netting and branch clipping have been informally compared to each other in terms of arthropod abundance (Smith and Robertson 2008) and arthropod biomass (Smith et al. 2006). Each method has also been compared to other methods in terms of arthropod biomass, abundance, and diversity (Majer et al. 1990, Buffington and Redak 1998, Doxon et al. 2011), but the precision, accuracy, and efficiency of these two methods have not been comprehensively assessed. Our objective, therefore, was to determine how well two commonly used sampling techniques precisely, accurately, and efficiently quantify food availability in forest habitats for American Redstarts (*Setophaga ruticilla*) specifically and insectivorous birds generally. Wintering American Redstarts (hereafter redstarts) attack flying and nonflying prey with near equal frequency in Jamaica (Lovette and Holmes 1995) and, therefore, choosing sampling methods directed at both prey types was important. We chose branch clipping and sweep netting because they are commonly used in forests (Poulin and Lefebvre 1997, Johnson 2000a, Studds and Marra 2005, Smith et al. 2006, Smith and Robertson 2008), designed to sample both active and sessile arthropods (Cooper and Whitmore 1990, Johnson 2000a), and inexpensive compared to suction devices (Cooper and Whitmore 1990).

Precision can be assessed by having multiple observers sample the same population to see if they arrive at the same result. Precision is important for longitudinal studies because multiple individuals are involved (e.g., different technicians over many years) and, therefore, individual bias may affect conclusions. To determine if the two methods are precise (i.e., lack individual bias), we examined the results of repeated sampling (by three individuals) using both sampling methods in redstart territories in two forest types, coastal mangrove forest, and scrub forest, in Jamaica.

Ideally, to assess the accuracy of a sampling technique, the estimate of the variable of interest is compared to a known value. In our study, arthropod biomass was unknowable because any measure of it requires use of a sampling technique of unknown accuracy. Instead, accuracy might be determined by comparing two methods to determine if they arrive at the same conclusion (although agreement of two methods is no guarantee of accuracy; Hutto 1990). Therefore, we assessed accuracy indirectly, by determining if the two methods were equally able to detect the absence of a predictable habitat-based difference in arthropod biomass.

Redstarts have been studied over the past 25 years at our study sites in Jamaica, and thus we can make reasonable *a priori* predictions about how the two habitats in our study area differ in arthropod biomass. Studds and Marra (2005, 2007, 2011) documented links between arthropod biomass and both redstart body condition and the timing of departure for spring migration. In most years, coastal mangrove habitat has greater arthropod biomass than scrub habitat, and birds in mangrove were consequently in better body condition and migrated earlier

than birds in scrub (Studds and Marra 2007). During our study (2009), however, we found no differences between habitats in redstart body condition or departure dates (N. W. Cooper, unpubl. data). Because body condition and departure date are closely linked to arthropod biomass (Studds and Marra 2005, 2007, 2011), we predicted similar levels of food availability in each habitat. Thus, we predicted that, if accurate, neither sampling method would detect a habitat-based difference in arthropod biomass.

Finally, efficiency of sampling techniques is important because the time available for field work and the associated costs are important limiting factors for researchers. To assess efficiency, we qualitatively described and compared the effort involved in collecting samples in the field and processing them in the lab to provide information concerning the amount of effort required for both sampling methods.

METHODS

Our study was conducted at the Font Hill Nature Preserve (18°02′ N, 77°57′ W) on the south coast of Jamaica and in Saint Elizabeth Parish between Whitehouse and Black River. Font Hill is a 249-ha wildlife reserve managed by the Petroleum Corporation of Jamaica. We sampled arthropods in two forest types: coastal mangrove and second-growth scrub. The coastal mangrove habitat (hereafter mangrove) is dominated by black mangrove (*Avicennia germinans)*, but both red (*Rhizophora mangle*) and white mangrove (*Laguncularia racemosa*) are present. Mangrove habitats are seasonally flooded by up to 1 m of water, and little understory vegetation is present except for the pneumatophores of black mangrove trees. In contrast, scrub habitat is dominated by logwood (*Haematoxylon campechianum*) and other deciduous trees (e.g., *Terminalia latifolia, Bursera simarubra*, and *Crescentia alata*), and has a well-developed understory of vines and other thorny plants including logwood saplings. Canopy trees in both habitats have many low limbs and much vegetation within the first 3 m of canopy. We conducted our study in April 2009 when both habitats were unusually dry, as indicated by the presence of little standing water in mangrove habitat and below-average rainfall (2009 $\bar{x}$ = 246 cm, 1994–2011 $\bar{x}$ = 368 cm) during the sampling period.

Sampling and sample processing. Arthropod samples were collected between 11:00 and 15:00 from 7 April 2009 to 13 April 2009. Because temperature and wind influence sweep-net samples (Hughes 1955), we collected all samples on sunny days with little wind. To test our hypotheses, we chose three individuals differing in size and strength: two males (NWC and MAT) and one female (MBG). NWC was 1.8 m tall and weighed 91 kg, MAT 1.8 m tall and 77 kg, and MBG 1.67 m tall and 66 kg. Each individual had similar experience with sweep netting and branch clipping, and all three sampled the same 24 redstart territories, 12 per habitat. To avoid sampling the same locations in a territory, one individual (NWC) sampled at the center of territories and the other two sampled locations 15 m away in a cardinal direction. Although vegetation structure was relatively homogenous in each habitat, sampling locations away from the center of each territory were inspected visually for structural similarity. Redstarts forage from the forest floor to the top of the canopy, but tend to focus on the lower to middle thirds (Sherry and Holmes 1997, Cooper, pers. obs.) and the canopy height of our study sites is relatively low (mangrove $\bar{x}$ = 9.1 ± 2.1 m, scrub $\bar{x}$ = 6.3 ± 1.5 m; N. W. Cooper, unpubl. data). Branch clipping and sweep netting took place 1–3 m above ground, thus overlapping areas where redstarts regularly forage.

Branch clipping creates less disturbance to the habitat so was used first, followed by sweep netting. Branch clipping (modified from Johnson 2000a) involved the use of garden clippers, a hooped canvas bag (diameter = 33 cm, depth = 66 cm), and a translucent plastic trash bag. Individual woody branches were selected at random from waist height to within reach of each individual (hereafter sampler). Samplers collected the outer 30 cm of branches to sample the same general area of trees as sweep netting (see below). Using a 30-cm piece of PVC pipe, the branch that was to be cut was measured from a distance, taking care not to disturb the branch or dislodge any arthropods. The canvas bag was then quickly placed over the branch and the bag closed by hand to seal the branch inside. A second individual then quickly cut the branch using the shears and inserted the remainder of the branch into the bag. The contents of the canvas bag were then transferred into the

plastic bag, making sure no arthropods escaped during the process. This process was repeated four times for a total of five 30 cm clippings per territory per sampler. These five branches represent one sample per territory. This amount was chosen to match the total amount of branch sampled by Johnson (2000a). One sample was taken at the center of each territory, and four others were taken 5 m away in the cardinal directions. When branch clipping, we disturbed surrounding vegetation as little as possible. Also, sweep netting was carried out in a 5-m circle around the center of each sampling location, whereas branch clipping took place at the center. This, along with the fact that sweep netting was done 15–20 min after branch clipping, should have minimized the potential for branch clipping to subsequently influence the sweep netting process by disturbing arthropods in the area.

The sweep net consisted of the same hooped canvas bag used above, but mounted to a 1.22 m wooden pole. The process consisted of slowly walking in a 5-m-radius circle around the center of each sampling location and swinging the sweep net at full force directly at green vegetation 20 times (Studds and Marra 2005). Swings were generally directed at the outer tips of branches and, because the diameter of the sweep net was 33 cm, we sampled roughly the same portion of the tree as with branch clipping. If there was more than a brief pause between swings, the bag was closed by hand to prevent arthropods from escaping. After 20 swings, the contents of the bag, including loose vegetation, were emptied into a plastic trash bag.

After freezing for at least 24 h, the three samplers searched their samples (up to 2 h each) for arthropods that were then placed in 70% ethanol in plastic (20 ml) scintillation vials and stored at room temperature. In the lab, NWC emptied each vial into a plastic (47 mm) petri dish and sorted all whole and partial arthropods from any dirt, spider webs, or other debris using a 75–15× dissecting scope.

We adjusted samples to reflect redstart diets by removing all isopterans (1 termite removed) and all arthropods > 10 mm in length (2 dragonflies removed) except for Lepidoptera larvae (Johnson 2000a). Arthropods were then transferred to aluminum weigh boats lined with glassine paper, oven-dried at 40°C for 24 h, and weighed (± 0.0001 g) using a digital scale (Ohaus Analytical Plus, Parsippany, NJ). We sorted all samples by order and, when possible, family into the following taxonomic groups for counts and to determine group-specific biomass: Heteroptera, Cicadellidae, Fulgoroidea, Psyllidae, Blattaria, Mantodea, Coleoptera, Diptera, Araneae, Lepidoptera, Pseudoscorpionida, Nueroptera, Orthoptera, Formicidae, and non-ant Hymenoptera.

Data analysis. To compare the two methods, we first determined the taxonomic groups that comprised ~75% of the samples by mass. We then used Mann–Whitney *U*-tests to compare arthropod biomass, abundance, and the proportion of flying insects sampled by the two methods for each habitat separately. To avoid pseudoreplication, Mann–Whitney *U*-tests were conducted separately for each sampler. Differences between methods were similar for each sampler and, therefore, only the results from one individual (NWC) are reported for these tests. Species accumulation curves were created to assess how each method sampled the habitats, except that we substituted our taxonomic groupings because we did not identify arthropods to species. The resulting taxon accumulation curves were created using EstimateS (Colwell 2009). We used the Fligner–Killeen test to compare the variance between the two methods (Donnelly and Kramer 1999).

We used generalized estimating equations (GEE) to test for sampler bias in estimating arthropod biomass and abundance. Separate analyses were conducted for each sampling method. Traditionally, researchers using branch clipping have divided the mass of arthropods in each sample by the mass of the branches and leaves clipped (Majer et al. 1990, Johnson 2000a) to produce a measure of arthropod density. However, because leaves of the two habitats we sampled differed in size and mass, we were cautious about making comparisons between habitats using a density measure that controls for leaf biomass. As a result, for all GEE analyses of branch clipping, we report results using both the raw arthropod biomass per sample (mg arthropods) and the more traditional density measure (mg arthropods/g vegetation) to evaluate the appropriateness of each measure.

Distributions of arthropod biomass and abundance did not meet assumptions of normality (Field 2005), and a Tweedie distribution with a log link best fit the data. Quasi likelihood under independence criterion (QIC) values were used to select the appropriate distribution and

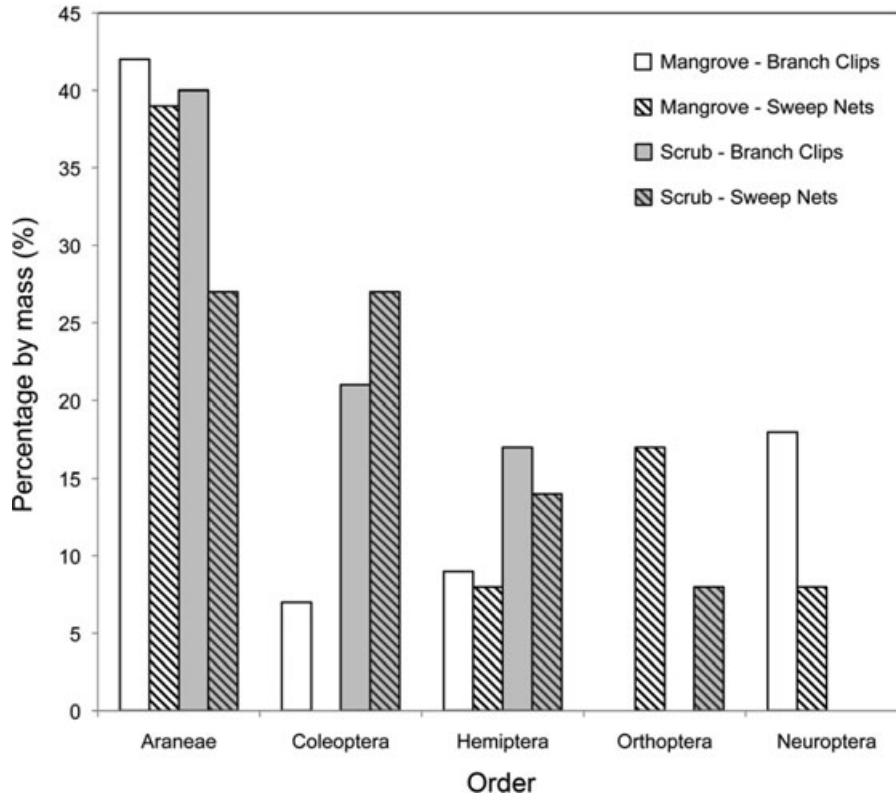

Fig. 1. Most common (~75% of total biomass) arthropod taxa in mangrove (unshaded) and scrub (shaded) habitats in Jamaica sampled by branch clipping (no pattern) and sweep netting (diagonal lines).

working correlation matrix (Pan 2001). In the GEE model, we entered sampler as a repeated measure and habitat as a fixed factor. Because we suspected that differences between samplers in sweep-net samples might be due to differences in strength or technique, we also compared the weight of vegetation sampled by each sampler using a Kruskal–Wallis ANOVA.

PASW 18.0 (SPSS Inc., Chicago, IL) (PASW 2010) was used for most statistical analyses. However, we used program R (R Development Core Team 2008) to conduct the Fligner–Killeen test for homogeneity of variances. Bonferroni corrections were carried out for all pair-wise comparisons in GEE. Means are reported ± 1 SD.

RESULTS

We collected 144 samples (12 territories in each habitat, sampled by three people, each using two methods) consisting of ~1800 arthropods representing 15 taxonomic groups. Most samples (~75% by mass) collected using each method consisted of similar taxa. In scrub habitat, arthropods in the orders Araneae, Coleoptera, and Hemiptera were sampled most often by both sweep netting and branch clipping, but sweep-net samples contained fewer Araneae and also included orthopterans (Fig. 1). In the remaining 25% of samples, we found no lepidopterans, dipterans, psuedoscorpions, or pysllids in branch-clip samples, whereas all these groups were sampled in small numbers (4 – 154 individuals) by sweep netting. In mangrove habitat, branch-clip samples contained primarily arthropods in the orders Araneae, Neuroptera, Hemiptera, and Coleoptera, whereas sweep-net samples consisted primarily of those in the orders Araneae, Orthoptera, Hemiptera, and Neuroptera (Fig. 1). As in scrub habitat, branch-clip samples in mangrove habitat

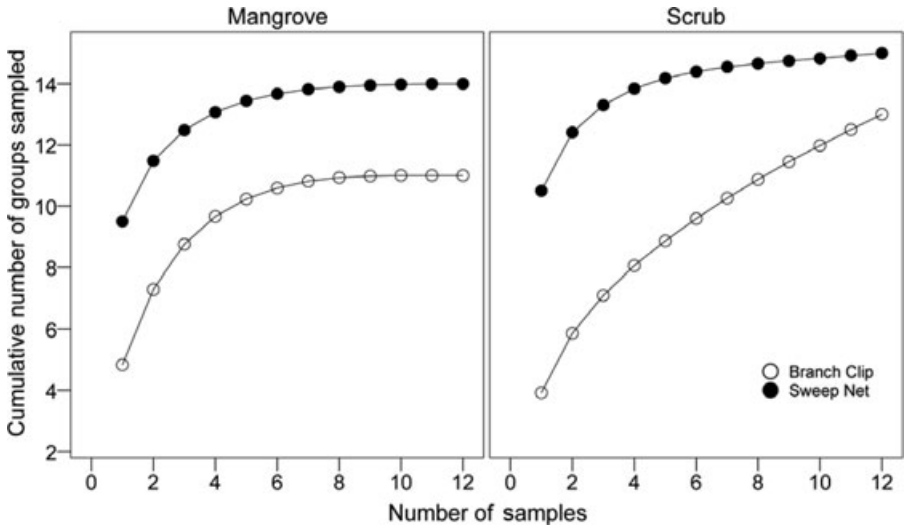

Fig. 2. Taxon (order or family) accumulation curves for sweep-net (closed circles) and branch-clip samples (open circles) in mangrove and scrub habitats in Jamaica.

missed several groups collected in small numbers (2–5 individuals) in sweep-net samples, including Formicidae, Lepidoptera, and Pseudoscorpionida. For all subsequent analyses, all arthropods (not just the top 75% by mass) were included.

The two methods differed in the proportion of flying insects captured in mangrove, but not in scrub, habitat. In mangrove, a higher proportion of flying arthropods was sampled by sweep netting (0.24 ± 0.13) than by branch clipping (0.14 ± 0.17; $U = 393$, $N = 69$, $P = 0.014$). In contrast, sweep netting (0.19 ± 0.11) and branch clipping (0.30 ± 0.35) did not differ in proportion of flying insects sampled in scrub habitat ($U = 580$, $N = 69$, $P = 0.86$).

The two methods differed in sampling completeness based on taxon accumulation curves. For mangrove, no new taxonomic groups were found after six samples for either method. However, sweep netting sampled 13 taxonomic groups, whereas branch clipping sampled only 11 taxonomic groups. In scrub, the sweep-netting curve reached an asymptote after seven samples, whereas the branch-clipping curve never reached an asymptote (Fig. 2).

More arthropods were sampled by sweep netting than by branch clipping, both in terms of biomass and abundance (Table 1), and sweep netting results were also less variable than those for branch clipping. Variation in arthropod biomass in the mangrove branch-clip samples (coefficient of variation [CV] = 89%) was greater than that in mangrove sweep-net samples (CV = 63%; Fligner–Killeen $\chi^2_1 = 21.2$, $P < 0.001$). Similarly, in scrub habitat, variation in branch-clip samples (CV = 102%) was greater than that in sweep-net samples (CV = 58%; Fligner–Killeen $\chi^2_1 = 28.9$, $P < 0.001$).

Precision and accuracy of sampling methods: arthropod biomass. For the branch-clipping method, our GEE model revealed no sampler effect on arthropod biomass (Wald $\chi^2_2 = 0.9$, $P = 0.62$). Arthropod biomass differed by habitat (Wald $\chi^2_1 = 7.4$, $P = 0.006$), with mangrove ($\bar{x} = 2.46 \pm 2.19$ mg) having greater arthropod biomass than scrub ($\bar{x} = 1.25 \pm 1.27$ mg). This difference remained significant after pairwise comparisons ($P = 0.006$). The habitat × sampler interaction was also significant (Wald $\chi^2_2 = 7.0$, $P = 0.03$), with MBG collecting similar arthropod biomass in scrub and mangrove and MAT and NWC collecting about twice as much biomass in mangrove as scrub.

Using arthropod density, the GEE analysis showed no significant sampler effect for the branch-clipping method (Wald $\chi^2_2 = 4.6$, $P = 0.10$). The habitat effect was significant (Wald $\chi^2_2 = 8.1$, $P = 0.004$), with scrub habitat (0.079 ± 0.122 mg arthropods/g vegetation)

Table 1. Mean (± SD) arthropod mass (mg) and abundance (number of individuals) collected in branch-clipping and sweep-netting samples in mangrove and scrub forests in Jamaica.

	Mangrove			Scrub		
	Branch clipping	Sweep netting	Significance	Branch clipping	Sweep netting	Significance
Biomass (mg)	2.9 ± 2.5	12.6 ± 6.7	$U = 13$, $P = 0.001$	1.1 ± 1.0	15.3 ± 6.5	$U = 0$, $P < 0.001$
Abundance (ind.)	5 ± 3.0	17 ± 9.7	$U = 15$, $P = 0.001$	4 ± 2.6	30 ± 11.6	$U = 1$, $P < 0.001$

having higher arthropod density than mangrove (0.028 ± 0.024 mg arthropods/g vegetation). The habitat × sampler interaction was significant (Wald $\chi^2_2 = 10.3$, $P = 0.006$) because MBG's samples showed a larger habitat difference than those of either MAT or NWC.

For sweep netting, the effect of sampler on arthropod biomass was significant (Wald $\chi^2_2 = 10.2$, $P = 0.006$), with MBG ($\bar{x} = 8.48 \pm 6.33$ mg) sampling less arthropod biomass than MAT ($\bar{x} = 11.22 \pm 6.44$ mg) and NWC ($\bar{x} = 13.97 \pm 6.62$ mg). After pairwise comparisons, the difference between MBG and NWC remained significant ($P = 0.005$), but no other pairwise differences were significant (MBG-MAT, $P = 0.14$; MAT-NWC, $P = 0.14$). Neither the effect of habitat (Wald $\chi^2_1 = 0.01$, $P = 0.94$) nor the habitat × sampler interaction effect was significant (Wald $\chi^2_2 = 5.2$, $P = 0.073$) for the sweep-netting method.

To determine if strength played a role in producing sampler bias in sweep netting, we measured the amount of vegetation sampled by each sampler. We found a difference in the amount of vegetation collected by each sampler by sweep netting in scrub ($\chi^2_2 = 28.1$, $P < 0.001$) and mangrove ($\chi^2_2 = 23.7$, $P < 0.001$) habitats. In both cases, MBG (Mangrove = 92.5 ± 35.1 g, Scrub = 9.3 ± 3.6 g) collected 3 to 9 times less vegetation than the other two samplers, whereas NWC (mangrove = 257.7 ± 61.5 g, scrub = 85.6 ± 27.6 g) and MAT (mangrove = 300.2 ± 85.7 g, scrub = 43.9 ± 20.9 g) collected similar amounts of vegetation.

Precision and accuracy of sampling methods: arthropod abundance. For branch clipping, we found that the effect of sampler (Wald $\chi^2_2 = 8.6$, $P = 0.013$) was significant, with NWC ($\bar{x} = 5.4 \pm 1.9$) collecting more arthropods per sample than MAT ($\bar{x} = 4.9 \pm 1.1$) and MBG ($\bar{x} = 3.8 \pm 1.9$). However, pairwise comparisons revealed that only the difference between MAT and MBG was significant ($P = 0.013$). The difference between MBG and NWC approached significance ($P = 0.059$), and there was no difference between MAT and NWC (P = 1.0). The effect of habitat (Wald $\chi^2_1 = 0.7$, $P = 0.40$) and the habitat × sampler interaction (Wald $\chi^2_2 = 2.1$, $P = 0.35$) were not significant.

For sweep netting, the effect of sampler on the number of arthropods sampled was not significant (Wald $\chi^2_2 = 3.5$, $P = 0.17$). However, arthropod abundance differed between habitats (Wald $\chi^2_1 = 5.7$, $P = 0.017$), with scrub ($\bar{x} = 25.6 \pm 14.4$ individuals) having greater arthropod abundance than mangrove ($\bar{x} = 18.6 \pm 10.4$ individuals; $P = 0.019$). We also found a significant interaction between habitat and sampler (Wald $\chi^2_2 = 7.9$, $P = 0.019$), with MBG sampling a similar number of arthropods as NWC and MAT in mangrove habitat, but sampling fewer arthropods in scrub habitat.

DISCUSSION

Branch clipping and sweep netting: sampler bias. We found significant sampler or habitat × sampler interaction effects for both branch clipping and sweep netting. The lack of precision in branch clipping was most likely due to differences between samplers in the height, species, or diameter of branches selected because other aspects of the method (e.g., closing the bag over the branch and transferring the sample to a trash bag) seem unlikely to have been carried out differently by the samplers. For sweep netting, the lack of precision was most likely due to differences in technique (see also O'Neill et al. 2002), strength, or endurance because the smallest sampler collected the least vegetation

per sample, and collected less arthropod biomass in both habitats and fewer arthropods in scrub.

Detection of habitat differences. Previous investigators have documented differences in arthropod abundance and biomass estimates produced by branch clipping and sweep netting. For example, Smith et al. (2006) found that branch clipping consistently revealed differences in arthropod biomass between habitats across the season, whereas sweep netting revealed differences at some times, but not others. In contrast, Smith and Robertson (2008) consistently detected the same habitat difference in arthropod abundance using both methods. Given relationships between arthropod biomass, overwinter body condition, and departure timing (Studds and Marra 2005, 2007, 2011), we predicted that, if accurate, neither method would reveal a difference between habitats in arthropod biomass in our study. However, with branch clipping, we found significant differences between habitats using arthropod biomass and arthropod density estimates, but in opposite directions. In contrast, we found no difference in arthropod biomass between the two habitats with sweep netting. Sweep netting thus appeared to more accurately detect the absence of a habitat-based difference in arthropod biomass. Reasons why investigators using these two methods have been able to detect differences in arthropod biomass between some habitats, but not others, remain unclear. However, factors such as the degree of similarity of vegetation profiles (e.g., amount of understory vs. canopy vegetation) and the species of plants and arthropods (e.g., flying vs. sessile) present in different habitats may influence arthropod biomass estimates.

Differences in taxa sampled. We obtained more diverse samples with sweep netting, and several taxa collected by sweep netting were not sampled by branch clipping. These differences may be due to differences between sampling methods in the likelihood of capturing certain types of prey or may have resulted only because less vegetation and fewer arthropods were sampled by branch clipping. However, Majer et al. (1990), sampling arthropods in Australian eucalypt forests, also found that branch clipping did not sample the entire range of arthropod diversity present. In addition, Johnson (2000a) found that branch clipping in citrus, coffee, and dry limestone habitats sampled flying insects in relatively small numbers. Because the results of previous studies suggest that American Redstarts attack flying insects more often in mangrove habitat than in other, drier habitats (Lovette and Holmes 1995), Johnson (2000a) suggested that branch clipping might not accurately determine the food resources available for redstarts in mangrove habitat. Our results support this assertion because, compared to sweep-net samples, flying insects were underrepresented in branch-clip samples. Other investigators have also found that fewer flying insects are captured with branch clipping than with sweep netting (Cooper and Whitmore 1990, Majer et al. 1990). Because sweep netting involves quicker, more active, and less predictable movements of a net, active insects may be less likely to escape.

Efficiency. We found that branch clipping took less time than sweep netting. Although sweep netting required only a few minutes (for 20 passes) and branch clipping took up to 10 min (to sample five branches) in the field, the sorting process for sweep netting in the lab was more time consuming. When removing arthropods from vegetation, branch-clip samples took no more than 15 min per sample, whereas sweep-net samples often required >60 min because sweep-net samples contained more arthropods and more vegetation. With fewer arthropods per sample, branch-clip samples could be sorted into taxonomic groups faster than sweep-net samples.

Although less time consuming than sweep netting, branch clipping resulted in the capture of fewer arthropods (both in terms of biomass and abundance). Other researchers have also noted that fewer arthropods were collected with branch clipping than with other methods, likely because branch clipping fails to capture as many mobile arthropods as other methods (Cooper and Whitmore 1990, Majer et al. 1990). However, branch clipping might sample as many arthropods as sweep netting if sampling effort was increased. In our study, assuming a roughly linear relationship between the number of samples and number of arthropods collected, we would have needed to clip four times more branches in mangrove (20 branches per territory), and 15 times more branches in scrub (75 branches per territory). This would increase time spent both in the field and the lab and, in addition, collecting so many branches might

negatively impact the habitat, at least for species like redstarts with small winter territories. Thus, such increases in the number of branches clipped may not be practical.

Conclusions and recommendations. The two methods used in our study produced different estimates of arthropod biomass and abundance, suggesting that the sampling method chosen may impact the results of a study. Although we found that branch clipping took less time, sweep netting was likely more accurate. Sweep netting also sampled a greater (but unknown) proportion of total arthropod diversity, which is important because several orders of arthropods preyed on by redstarts were not sampled by branch clipping. Finally, sweep-net samples also had lower coefficients of variation, which impacts the minimum sample size.

Because both arthropod density and biomass estimates determined by branch clipping appeared to be inaccurate in our study, we cannot determine which measure is better. However, the choice is not arbitrary because the two measures produced opposite conclusions about which habitat had more food resources for birds in our study. Previous researchers have used density estimates only (Johnson 2000a, b, Smith et al. 2006, Smith and Robertson 2008), and Cooper and Whitmore (1990) asserted that using density estimates allowed for direct comparisons between habitats. However, we feel that caution must be taken when comparing density estimates between habitats because of potentially large differences in leaf and branch mass, shape, size, and palatability. For example, in our study, scrub trees had small, thin deciduous leaves whereas mangrove leaves were much larger, thicker, and evergreen. Ultimately, we may not know enough about how arthropod biomass responds to vegetation biomass to use a density measure that incorporates vegetation biomass to compare arthropod communities across such different forests.

Despite its apparent advantages, sweep netting was sensitive to sampler bias and thus we recommend using either a single sampler or samplers similar in size and strength. We found significant differences between samplers in the amount of vegetation collected using sweep netting, and one possible way to control for this bias is to calculate arthropod density (mg arthropods/g of vegetation). If sampling only one habitat type, this may be appropriate. However, for between-habitat comparisons, this may not be appropriate because of differences in leaf and branch mass, and also because different species of trees may differ in the likelihood of shedding leaves when struck. Alternatively, multiple samplers could sample the same locations and sampler differences could be corrected statistically. Additionally, taking efforts to standardize the swinging technique may lead to greater precision (O'Neill et al. 2002).

Our study highlights the importance of choosing the most precise, accurate, and efficient arthropod sampling method to measure arthropod resources. However, not all forest habitats are alike and branch clipping or other methods like suction devices may be more practical in some forest types (e.g., tall canopies with little understory vegetation). We recommend that researchers evaluate the precision, accuracy, and efficiency of several sampling methods prior to broad application in their study systems.

ACKNOWLEDGMENTS

We thank C. Tonra and S. Wilson for help with study design, and R. Schneider and three anonymous reviewers for helpful comments on an earlier version of the manuscript. D. Corey's assistance with statistical analysis is greatly appreciated. We thank the Petroleum Corporation of Jamaica and the Font Hill staff for access to the field site. PPM and T. Sherry supported all research with a grant from the National Science Foundation.

LITERATURE CITED

Brown, D. R., and T. W. Sherry. 2006a. Behavioral response of resident Jamaican birds to dry season food supplementation. Biotropica 38: 91–99.

———, and ———. 2006b. Food supply controls the body condition of a migrant bird wintering in the tropics. Oecologia 149: 22–32.

Buffington, M. L., and R. A. Redak. 1998. A comparison of vacuum sampling versus sweep-netting for arthropod biodiversity measurements in California coastal sage scrub. Journal of Insect Conservation 2: 99–106.

Burke, D. M., and E. Nol. 1998. Influence of food abundance, nest-site habitat, and forest fragmentation on breeding Ovenbirds. Auk 115: 96–104.

Colwell, R. K. [online]. 2009. EstimateS 8.20: statistical estimation of species richness and shared species from samples. <http://purl.oclc.org/estimates> (16 August 2010).

Cooper, R. J., and R. C. Whitmore. 1990. Arthropod sampling methods in ornithology. Studies in Avian Biology 13: 29–37.

DONNELLY, S. M., AND A. KRAMER. 1999. Testing for multiple species in fossil samples: an evaluation and comparison of tests for equal relative variation. American Journal of Physical Anthropology 108: 507–529.

DOXON, E. D., C. A. DAVIS, AND S. D. FUHLENDORF. 2011. Comparison of two methods for sampling invertebrates: vacuum and sweep-net sampling. Journal of Field Ornithology 82: 60–67.

FIELD, A. 2005. Discovering statistics using SPSS. Sage Publications, London, UK.

GILL, F. B. 2006. Ornithology. W. H. Freeman, New York, NY.

HUGHES, R. D. 1955. The influence of prevailing weather on the numbers of *Meromyza variegata* Meigen (Diptera, Chloropidae) caught with a sweepnet. Journal of Animal Ecology 24: 324–335.

HUTTO, R. L. 1990. Measuring the availability of food resources. Studies in Avian Biology 13: 20–28.

JOHNSON, M. D. 2000a. Evaluation of an arthropod sampling technique for measuring food availability for forest insectivorous birds. Journal of Field Ornithology 71: 88–109.

———. 2000b. Effects of a shade-tree species and crop structure on the winter arthropod and bird communities in a Jamaican shade coffee plantation. Biotropica 32: 133–145.

———, AND T. W. SHERRY. 2001. Effects of food availability on the distribution of migratory warblers among habitats in Jamaica. Journal of Animal Ecology 70: 546–560.

KARR, J. R. 1976. Abundance of migrants from the North Temperate Zone in tropical habitats. Wilson Bulletin 88: 433–458.

LOVETTE, I. J., AND R. T. HOLMES. 1995. Foraging behavior of American Redstarts in breeding and wintering habitats: implications for relative food availability. Condor 97: 782–791.

MAJER, J. D., H. F. RECHER, W. S. PERRIMAN, AND N. ACHUTHAN. 1990. Spatial variation of invertebrate abundance within the canopies of two Australian eucalypt forests. Studies in Avian Biology 13: 65–72.

MORRIS, R. F. 1960. Sampling insect populations. Annual Review of Entomology 5: 243–264.

MURPHY, M. T. 1986. Temporal components of reproductive variability in Eastern Kingbirds (*Tyrannus tyrannus*). Ecology 67: 1483–1492.

O'NEILL, K. M., D. P. LARSON, AND W. P. KEMP. 2002. Sweep sampling technique affects estimates of the relative abundance and community composition of grasshoppers (Orthoptera: Acrididae). Journal of Agricultural and Urban Entomology 19: 125–131.

PAN W. 2001. Akaike's information criterion in generalized estimating equations. Biometrics 57: 120–125.

PASW. 2010. PASW 18.0 for Mac OS X. Release 18.03. SPSS, Inc., Chicago, IL.

POULIN B., AND G. LEFEBVRE. 1997. Estimation of arthropods available to birds: effect of trapping technique, prey distribution, and bird diet. Journal of Field Ornithology 68: 426–442.

R DEVELOPMENT CORE TEAM. 2008. A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.

RODENHOUSE, N. L., AND R. T. HOLMES. 1992. Results of experimental and natural food reductions for breeding Black-throated Blue Warblers. Ecology 73: 357–372.

SHERRY, T. W., AND R. T. HOLMES. 1997. American Redstart (*Setophaga ruticilla*). In: The birds of North American online (A. Poole, ed.). Cornell Lab of Ornithology, Ithaca, NY.

———, M. D. JOHNSON, AND A. M. STRONG. 2005. Does winter food limit populations of migratory birds? In: Birds of two worlds: the ecology and evolution of migration (R. Greenberg and P. P. Marra, eds.), pp. 414–25. Johns Hopkins University Press, Baltimore, MD.

SMITH, A. L., AND R. J. ROBERTSON. 2008. Seasonal changes to arthropod abundance in successional forests of the Yucatan Peninsula, with implications for overwintering forest birds. Ornitologia Neotropical 19: 81–95.

SMITH, L. A., D. M. BURKE, E. NOL, AND K. A. ELLIOTT. 2006. The effects of partial cutting on the Rose-breasted Grosbeak: abundance, food availability, and nest survival. Canadian Journal of Forest Research 36: 1087–1097.

SOUTHWOOD, T. R. E. 1978. Ecological methods. Chapman and Hall. London, UK.

STUDDS, C. E., AND P. P. MARRA. 2005. Nonbreeding habitat occupancy and population processes: an upgrade experiment with a migratory bird. Ecology 86: 2380–2385.

———, AND ———. 2007. Linking fluctuations in rainfall to nonbreeding season performance in a long-distance migratory bird, *Setophaga ruticilla*. Climate Research 35: 115–122.

STUDDS, C. E., AND P. P. MARRA. 2011. Rainfall-induced changes in food availability modify the spring departure programme of a migratory bird. Proceedings of the Royal Society B 278: 3437–3443.